VENATION PATTERNS IN THE LEAVES OF EPHEDRA

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THE VIEW IS WIDELY HELD that the vascular supply of the leaf in *Ephedra* consists of two traces associated with a unilacunar type of node (Marsden & Steeves 1955). This interpretation has brought *Ephedra* prominently into recent discussions of the phylogenetic status of the unilacunar, two-trace type of vasculature which occurs not only in *Ephedra* and certain other gymnosperms but which is also characteristic of the cotyledonary and foliage-leaf nodes of a number of dicotyledons (Marsden & Bailey 1955; Bailey 1956).

The considerable attention which has been devoted to the nodal anatomy of *Ephedra* has not been accompanied by comparably detailed studies on the foliar venation in any of the numerous species of this genus. This overt neglect of venation probably is due in large part to the fact that the very small "reduced" leaves, apparently characteristic of the majority of species, have not seemed very promising types of appendages for detailed comparative studies. My survey of the voluminous literature on *Ephedra* failed to reveal a single drawing or photomicrograph illustrating the venation pattern as it would appear in cleared, stained foliage leaves. As far as I could discover, the great majority of previous descriptions of leaf venation in *Ephedra* were based on reconstructions derived from a study of serial transections of buds or mature nodes. One of the few exceptions which I have encountered occurs in the recent paper by Lehmann-Baerts (1967) who made considerable use of cleared and stained whole mounts in her study of "tracheogenesis" in the paired veins of developing cotyledons and primary leaves of several species of *Ephedra*. It is also evident that Scheit (1883) employed clearing techniques in his study of venation and transfusion tissue in the leaves of *Ephedra altissima* and *Gnetum gnemon*.

On the basis of the information provided by serial transections, the great majority of investigators reached the conclusion that the venation of an *Ephedra* leaf consists of a pair of veins which neither branch nor anastomose during their course through the sheath and lamina (Marsden & Steeves 1955, p. 244; Napp Zinn 1966, pp. 173–174). The largely neglected investigations of Monoyer (1937; 1938, a, b, c) however, revealed for the first time that the leaf trace in certain species of *Ephedra* may be trifasciculate. In most of the species he studied, only the two lateral members of the trifasciculate trace extend into the leaf while the median trace ends at the nodal girdle as the result of an arrest in its upward development, a process which Monoyer (1938, b, c) termed "acrolysis." But in *E. fragilis* var. *campylopoda*, Monoyer (1937) found that *each* member of a leaf pair consistently has three veins, a median

"M" and two lateral veins, "L,L." This unusual type of venation is illustrated in his paper by drawings of transections at two different levels through a bud (see Monoyer 1937, *plate II, Figs. 1, 2*). Monoyer's studies led him to conclude that the three-veined type of vasculature may represent the "primitive" condition in *Ephedra* and that the more common two-veined condition is derivative.

The occurrence of three-trace leaves, as reported by Monoyer, raises important but as yet unsolved questions concerning nodal evolution and venation in the genus as a whole. In their survey of nodal anatomy in nine species of *Ephedra*, Marsden & Steeves (1955, *Text-figs. 3–5*) described and illustrated, for both decussate and whorled phyllotaxies, the presence of internodal "complementary bundles" comparable in position to Monoyer's median leaf traces. Marsden & Steeves also noted that the complementary bundles usually extend from one nodal girdle to the next "without in any way joining the leaf traces." In rare instances (e.g. *E. altissima*) however, they found that "the complementary bundle extends into the leaf as a third trace."

In the light of the conflicting interpretations of leaf venation in *Ephedra*, I decided to explore as thoroughly as possible, the venation patterns of a species in which complementary bundles and three-veined leaves occur. A preliminary examination of available cultivated material indicated that *E. chilensis* Miers would be suitable for study, especially since the nodal and internodal anatomy of this taxon had already been analysed in detail by Marsden & Steeves (1955, *Text-fig. 5*). The other two species included in the present study, *E. foliata* Boiss. and *E. altissima* Desf., were chosen because in both the leaf fluctuates greatly in size, in some cases reaching a length of 1.5 to 2 cm. The conspicuous variation in leaf dimensions allows one to compare the venation patterns of scale-like leaves with those of the well-developed needle-like leaves.

MATERIALS AND METHODS

Material of the three species of *Ephedra* included in my study was obtained from the following sources: *E. foliata* (1) shoots from plants growing in the University of California Botanical Garden at Berkeley and in the Botanical Garden, University of Delhi, India, and (2) specimens from the herbarium of the University of California, Berkeley (*Barkley 32 Ir 2299; Stewart 14663A*); *E. altissima*, shoots from plant No. 79214 growing at the Plant Introduction Station, Chico, California; *E. chilensis*, cultivated plant No. 49542 in University of California Botanical Garden (voucher specimens deposited in U. C. Herbarium). It is a great pleasure to express my thanks to Dr. B. M. Johri for the preserved material of *E. foliata* and to Dr. R. L. Smith for the living specimens of *E. altissima*.

Individual leaves, removed from the nodes by tangential longitudinal cuts, as well as nodal segments with attached leaves, were cleared by prolonged treatment in 5–10% NaOH followed, after thorough washing in water, by chloral hydrate. The leaves and nodal sectors of living ma-

terial which had been fixed in 50% alcohol or formalin-acetic acid-alcohol were more refractory than herbarium specimens and it was necessary to accelerate the clearing phase in NaOH by placing the specimens in petri dishes on an electric slide-warmer for long periods of time.

Very instructive preparations of *E. chilensis*, showing the complete venation of each member of a leaf-pair and the basal connections of the respective leaf traces were secured by making careful longitudinal cuts between the leaves and through the node and subjacent internode of cleared segments of the shoot. The separated halves were then dehydrated in the usual alcohol series and stained for several hours in a 1% solution of safranin in equal parts of absolute alcohol-xylene. After destaining in alcohol-xylene, the specimens were mounted in "Piccolyte." Similar procedures were followed in processing and staining detached leaves of all the species included in the present study.

Satisfactory photomicrographs of *E. chilensis* showing clearly the venation pattern and the mode of attachment of the leaf traces proved difficult to obtain by means of transmitted light because of the very numerous fibers adjacent to the veins in the leaf sheath region. The problem was solved by Mr. A. A. Blaker who employed a combination of directional dark field and transmitted light in which the dark field is oriented along the longitudinal axis of the specimen. Under these lighting conditions, the veins, leaf traces, and internodal vascular strands appear brilliantly refractive and distinct from the fibers and other tissues (see PLATES IV, V). I wish to thank Mr. Blaker for his skillful preparation of these illustrations as well as for the other photomicrographs used in this paper.

LEAF MORPHOLOGY

In the genus *Ephedra* which comprises about 35 described species (Markgraf 1926), the leaves occur in pairs or whorls at each node and are basally connate, forming a more or less conspicuous sheath. Napp-Zinn (1966, p. 173) uses the term "gamophyll" to designate the fused character of the leaves. Although the classical monographs of Meyer (1849) and Stapf (1889) plainly reveal the considerable fluctuation in the size and proportion of the lamina in *Ephedra* leaves, this variability is either minimized or disregarded in many modern descriptions. A few typical examples of misleading generalizations will be given to illustrate this point. Pearson (1929, pp. 1, 2), in his well known monograph on the Gnetales, states that in *Ephedra* "the assimilating stems are slender and grooved and bear whorls of reduced leaves; they clearly resemble the aerial shoots of *Equisetum*." But he adds that in *E. altissima, E. foliata,* and *E. gracilis,* the leaf blade "is developed only at the middle and the upper nodes." Another vague description occurs in Chamberlain's (1935) text on the gymnosperms, in which it is stated that "the leaves are small and rudimentary, and, even when young, are of scarcely any importance in the vegetative economy of the plant." Zimmermann (1959,

p. 460) and Sporne (1965, p. 184), respectively, describe the foliage of *Ephedra* as "decussate scale-leaves" and as "reduced to minute scales."

In contrast to these characterizations, Stapf (1889) noted that although in the majority of species the leaves are reduced to sheaths, a well-developed lamina occurs in some leaves of *E. altissima, E. foliata, E. gracilis,* and *E. americana* var. *andina,* reaching in individual cases a length of 3 cm. and a width of 1 to 1.5 mm. In all these species, the lamina is delicate and ultimately abscisses from the persistent sheath. It seems likely that the persistent sheathing bases of the leaves of herbarium specimens may often be mistaken for *complete* "scale-leaves."

It will now be appropriate to describe briefly the results of the present investigation on leaf morphology. A well-developed leaf in both *E. foliata* and *E. altissima* consists of a basal sheath, joined by a membranous commissure with the other leaf or leaves at the node, and a subulate lamina (TEXT-FIG. 3; PLATE I: 1, 3, 4). The total length (i.e. sheath + lamina) of leaves of this type varies considerably; small leaves, with weakly-developed laminae, measure only 8 to 9 mm. in length while the longest leaves studied are 1.5 to 2 cm. long. No examples of leaves 2.5 to 3 cm. long, as found by Stapf (1889) in *E. foliata,* were encountered in the present study. In both *E. altissima* and *E. foliata,* the foliar appendages of the basal nodes of the shoot tend to be relatively small, with laminae measuring only 3 to 4 mm. in length (TEXT-FIG. 4). There is obviously however, no sharp demarcation between "well-developed" and scale-like leaves. Very commonly a single shoot during its development may form a graded series of appendages, with the smaller leaves at the base and the longer, better developed leaves restricted to nodes in the middle region.

The *consistently* smaller laminae of the leaves of *E. chilensis* correspond to some of the current descriptions regarding the "reduced" nature of *Ephedra* leaves. In *E. chilensis* the phyllotaxis is variable in a single individual: well-developed shoots commonly — although not invariably — form three-leaved whorls whereas the leaf arrangement on the more slender lateral shoots is usually decussate. Regardless of phyllotaxis, the leaf consists of a prominent sheath and an extremely small lamina (TEXT-FIG. 5; PLATES IV–VI). In my material, the average length of the leaf is approximately 5 mm., a dimension which falls within the size range of 4.1 to 6.1 mm. noted by Miers (1869, pp. 164, 165) in his description of *E. chilensis.*

VENATION PATTERNS

Review of Literature. As I have indicated in the introduction of this paper, the consensus of opinion in the literature is that the venation of the leaves (including the cotyledons) of *Ephedra* consists of two unbranched veins which represent the upward extension of a pair of leaf traces (TEXT-FIG. 1). In a comprehensive survey of the old as well as the modern literature I have been struck by the vague and extremely brief descriptions of this venation pattern. It would be tedious to review

chronologically the various statements because of their repetitive character (see for example, the descriptions given by Thompson 1912, Goebel 1932, Troll 1938, Campbell 1940, Marsden & Steeves 1955, and Sporne 1965). It was particularly surprising to find that in Pearson's (1929) description of *Ephedra*, no mention is made of foliage-leaf venation. His account of vasculature in the adult shoot is strictly limited to nodal anatomy and the course of the double leaf traces in the eustele.

Many authors, who make a casual reference to venation, describe the venation of an *Ephedra* leaf as "parallel." Geyler (1867–68, p. 142) for example, in his classical paper on leaf-trace systems in gymnosperms, stated with reference to *E. equisetiformis* that the two bundles belonging to the leaf trace "extend together parallel and unbranched in the leaf." Similar descriptions of "parallel" venation in *Ephedra* were subsequently repeated by Bertrand (1874), Stapf (1889), Voth (1934), and Maheshwari & Vasil (1961). Eames (1952, p. 92) was particularly impressed by the course of the leaf veins in *Ephedra* and remarked: "The parallel-veined linear leaf resembles that of the cordaites and conifers in general type. It usually has two traces, typically widely separated in origin, though in some species there are said to be two traces arising side by side, or there may be only one trace. In the cordaites also the leaf has one or two traces."

As indicated previously, doubt as to whether the two-trace pattern of foliar vasculature is consistent throughout the genus *Ephedra* arose through the investigations of Monoyer (1937, 1938, a, b, c). His observation that the leaves of *E. fragilis* var. *campylopoda* are provided with an additional vein situated between the two lateral veins, raises important questions which I will discuss later in the paper. For purposes of general orientation, however, reference at this point should be made to TEXT-FIGURE 2 which illustrates the three-veined pattern which I have found in certain leaves of *E. chilensis*.

Venation Patterns in Ephedra foliata and E. altissima. The vasculature of the leaves of these species consists of two veins which either terminate freely near the leaf apex or are connected by transfusion tracheids at variable levels in the lamina (PLATES I and II). This fundamental similarity in venation patterns is interesting from a systematic viewpoint because Stapf (1889, p. 35) included both species in the "Tribus *Scandentes*" under the section PSEUDOBACCATAE. In his opinion, the "Tribus *Scandentes*" comprises "a very natural group" of species.

The comparative study of venation patterns in a relatively large number of cleared stained leaves emphasizes that the veins are not "parallel" in their course through the leaf, as has been repeatedly asserted in the general literature on *Ephedra*. On the contrary, the two veins, which may be either widely spaced or closely approximated in the leaf sheath, progressively *converge* towards the lamina-apex (PLATE I).

A salient feature of leaf anatomy in *Ephedra foliata* and *E. altissima* is the more or less profuse development of "transfusion tracheids." This term is used to designate the relatively short box-shaped cells, with reticu-
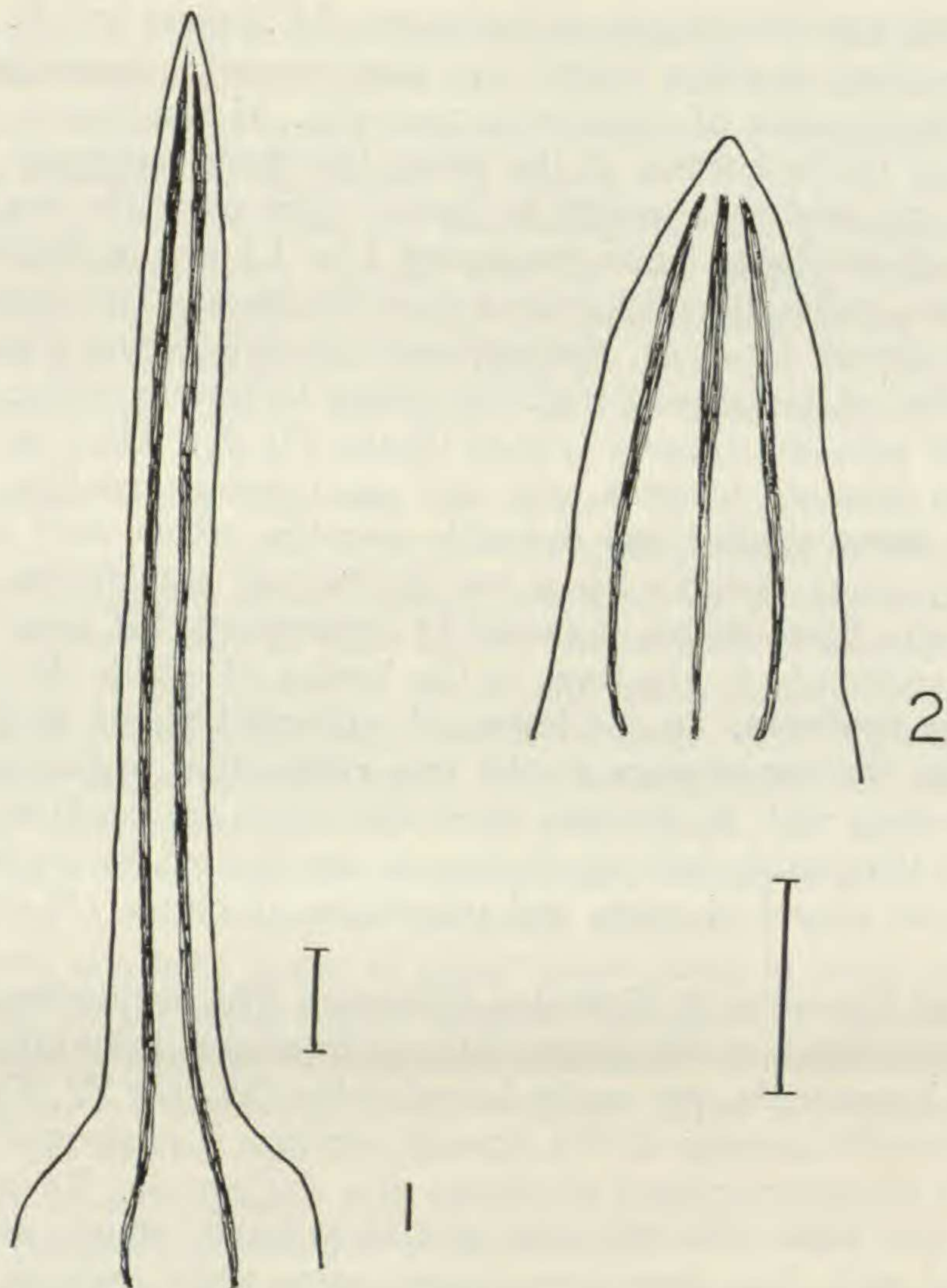
FIGURES 1, 2. Contrasted patterns of open leaf venation in *Ephedra*. FIGURE 1, two-veined leaf of *Ephedra foliata*. FIGURE 2, three-veined leaf of *E. chilensis*. The scale near each drawing equals 1 mm.

late or reticulate-pitted walls which occur along the borders of the xylem strands and which in many cases form a compact tissue between the vein tips (PLATE II: 5–7). As far as I am aware, Scheit (1883, p. 626) was the first to observe and describe the transfusion tracheids in the leaf of *E. altissima*. He introduced the term "tracheid-border" ("Tracheid-ensaüme") to designate the wing-like extensions of tracheids associated with the foliar veins of certain gymnosperms. In *E. altissima*, according to Scheit, reticulately thickened tracheids cover the vein endings as a cap-like mass of cells. The occurrence of transfusion tracheids in this species was also briefly noted by Thompson (1912, p. 1098). But since he relied on leaf transections rather than cleared leaves, he greatly underestimated the abundance of transfusion tracheids by stating that "at the edges of the bundle, as Strasburger has noted, there is an occasional transfusion tracheid which can be distinguished by its bordered pits and thickening bars."

The general venation pattern of the leaves of *E. foliata* and *E. altissima* may be described as either "open" or "anastomosed," depending on the degree of development of transfusion tracheids. If transfusion tracheids are restricted to the borders of the veins, the latter terminate freely at the lamina apex and the venation is "open." This condition has been observed in well-developed leaves measuring 1 to 1.5 cm. in length as well as in the more rudimentary laminae of scale-like leaves (TEXT-FIG. 1, 3, 4; PLATE I: 1, PLATE II: 5, 6). Anastomosed venation occurs when the adjacent borders of transfusion tracheids merge to form a wedge of tissue between the vein-tips (PLATE I: 2–4; PLATE II: 7). There is no sharp demarcation however, between open and anastomosed venation. A number of the leaves studied had definable vein-tips which were joined for only a very short distance by a few intervening transfusion tracheids (PLATE I: 4). Furthermore, it should be emphasized that great variation exists with reference to the level in the lamina at which the two veins first become confluent. In the leaves of cultivated plants of *E. foliata*, for example, the convergence of the two veins often begins well below the lamina-apex and, in extreme cases, the veins are confluent at such a low level that nearly half the lamina is vascularized by an apparently single massive strand of xylem and transfusion tracheids (PLATE II: 8).

Venation Patterns in Ephedra chilensis. The distinctive feature of the foliar vasculature of this species is the interpolation, in certain leaves, of a midvein between the two major lateral veins (PLATES IV, V). One of the most puzzling aspects of this type of venation is its sporadic and unpredictable occurrence among the leaves of a single node. TEXT-FIGURE 5 illustrates this point with reference to a three-leaved whorl: one leaf, B, is provided with three freely-terminating veins while each of the other two leaves is vascularized by a pair of veins as shown in A. Comparable variations seem to occur even more frequently in relation to decussate phyllotaxis. Most commonly, both members of a leaf-pair are two-veined but in some of the cleared nodal sectors, one leaf may possess a midvein while the other appendage conforms to the predominant two-veined pattern of vasculature (PLATE IV, A, B). Only a single example was found in which *both* members of a leaf-pair were three-veined.

In order to compare the nodal anatomy of two- and three-veined leaves in *E. chilensis*, selected nodal segments were split longitudinally and the two halves stained in safranin. Preparations of this type clearly reveal the independence between the complementary bundle and the traces which supply a two-veined leaf. As is shown in PLATE III, the complementary bundle terminates abruptly in a mass of transfusion tracheids at the node whereas the two leaf traces are attached to separate parts of the eustele. On this point, my observations fully agree with the reconstruction of nodal and internodal vasculature diagrammatically shown by Marsden & Steeves (1955, *Text-fig. 4*). The nature of the vascular connections of three veined leaves in *E. chilensis*, however, was not included in their description and illustrations of the nodal anatomy of this species. During the present

investigation, a number of successful preparations of divided nodal segments were obtained which show the contrast in nodal anatomy and venation which frequently occurs between members of a leaf-pair. A representative example of my results is shown in PLATE IV. In the three-veined leaf at the left (leaf A), the strong midvein is basally connected with the complementary bundle and the two lateral veins are joined independently to the stele in exactly the same manner as the traces of the two-veined leaf shown at the right (leaf B). Whether the midvein of leaf A represents the "foliar extension" of the complementary bundle or whether the latter simply provides a point of attachment for the midvein, are questions which can only be settled by appropriate ontogenetic studies.

An interesting, but unanticipated, result of my studies on *E. chilensis* was the discovery that in some leaves, the midvein terminates blindly at various levels in the lamina or sheath and hence fails to establish a connection with a complementary bundle (PLATE VI). Various types of "transitions" occur between leaves with basally connected midveins and those with "suspended" midveins. In some leaves, the basal connection between the midvein and the complementary bundle is tenuous and consists only of a file of slender tracheary elements (PLATE V: 11). Examples have also been found of three-veined leaves in which the midvein ends blindly in the nodal region between the points of attachment of the lateral traces (PLATE V: 12). Leaves with these venation patterns clearly seem to provide "connecting links" with the types of venation depicted in PLATE VI. Under high magnification, the basal end of a suspended midvein is usually slender and consists of a few elongated, helically-thickened tracheary elements (PLATE VII: 16).

This description of venation patterns in *Ephedra chilensis* may appropriately conclude with a few comments on the occurrence of transfusion tracheids. As shown in PLATES IV and V, transfusion tracheids are abundant in both two- and three-veined leaves. Very often, as shown in these illustrations, the vein-tips are "embedded" in a voluminous mass of transfusion tracheids. In the lower portion of the lamina, where the veins are well-separated, each vein is laterally flanked by continuous or interrupted files of conspicuous box-shaped transfusion tracheids (PLATE VII: 15). Cells of this type may be so abundant in the upper region of the leaf that the boundaries between adjacent veins are difficult or impossible to determine (PLATE IV: A; PLATE V: 12).

DISCUSSION

One of the most important conclusions of the present study is that the venation pattern is variable not only between the leaves of different species but, as in *Ephedra chilensis*, even between the members of the same whorl or pair of leaves (TEXT-FIG. 5; PLATE IV). This variability has received very little attention in the past (see "Review of Literature," p. 367). In most descriptions, the venation is said to consist of a pair of
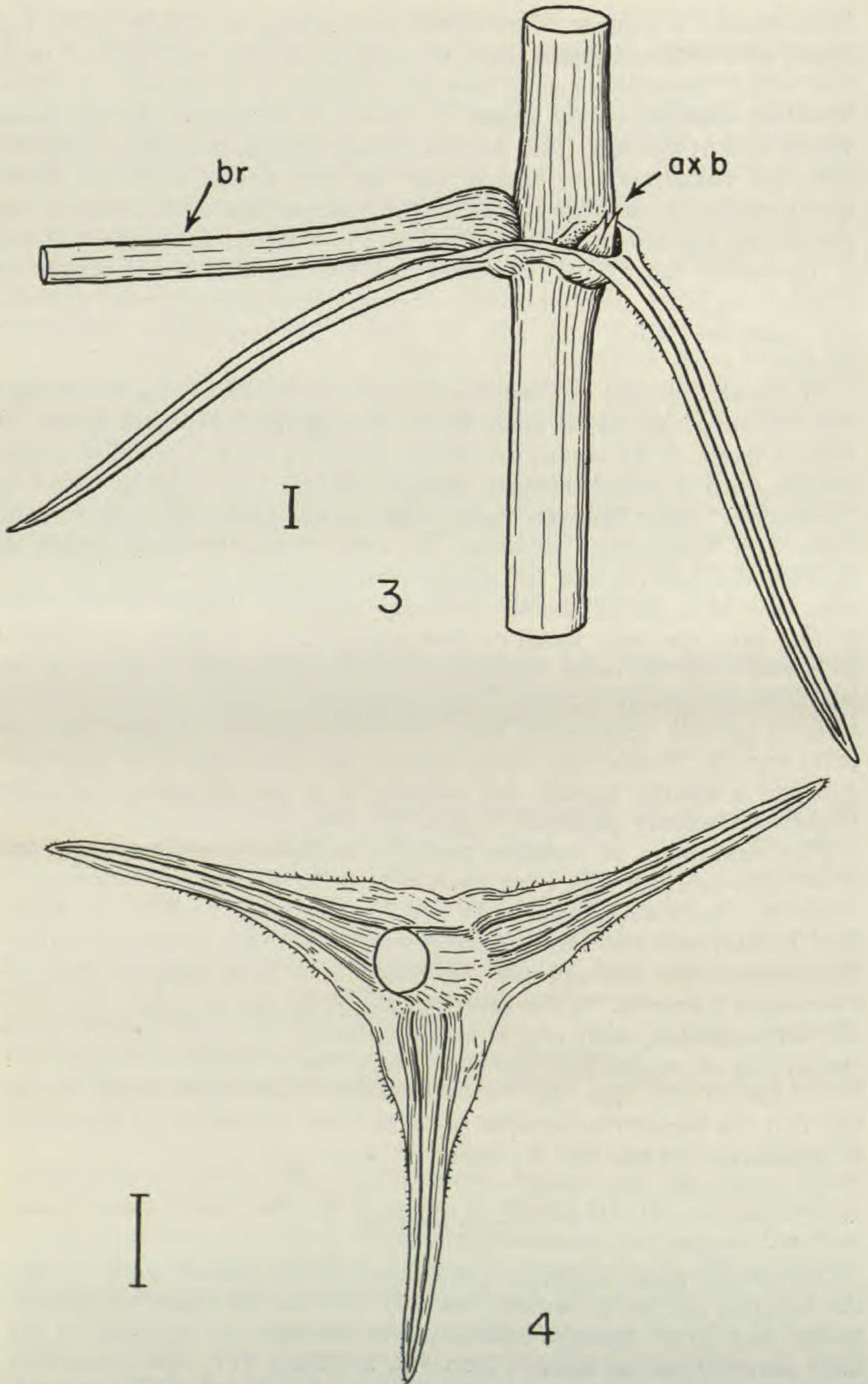
FIGURES 3, 4. Variations in size and morphology of leaves in *Ephedra foliata*
(*Barkley 32 Ir 2299*, UC). FIGURE 3, leaves with well-developed laminae and

free "parallel," veins which represent the upward extension of two leaf traces associated with a single gap. It is now clear, however, that the variation in venation pattern in *Ephedra* includes differences in both the number of veins — two or three — as well as the mode of termination of the veins in the lamina.
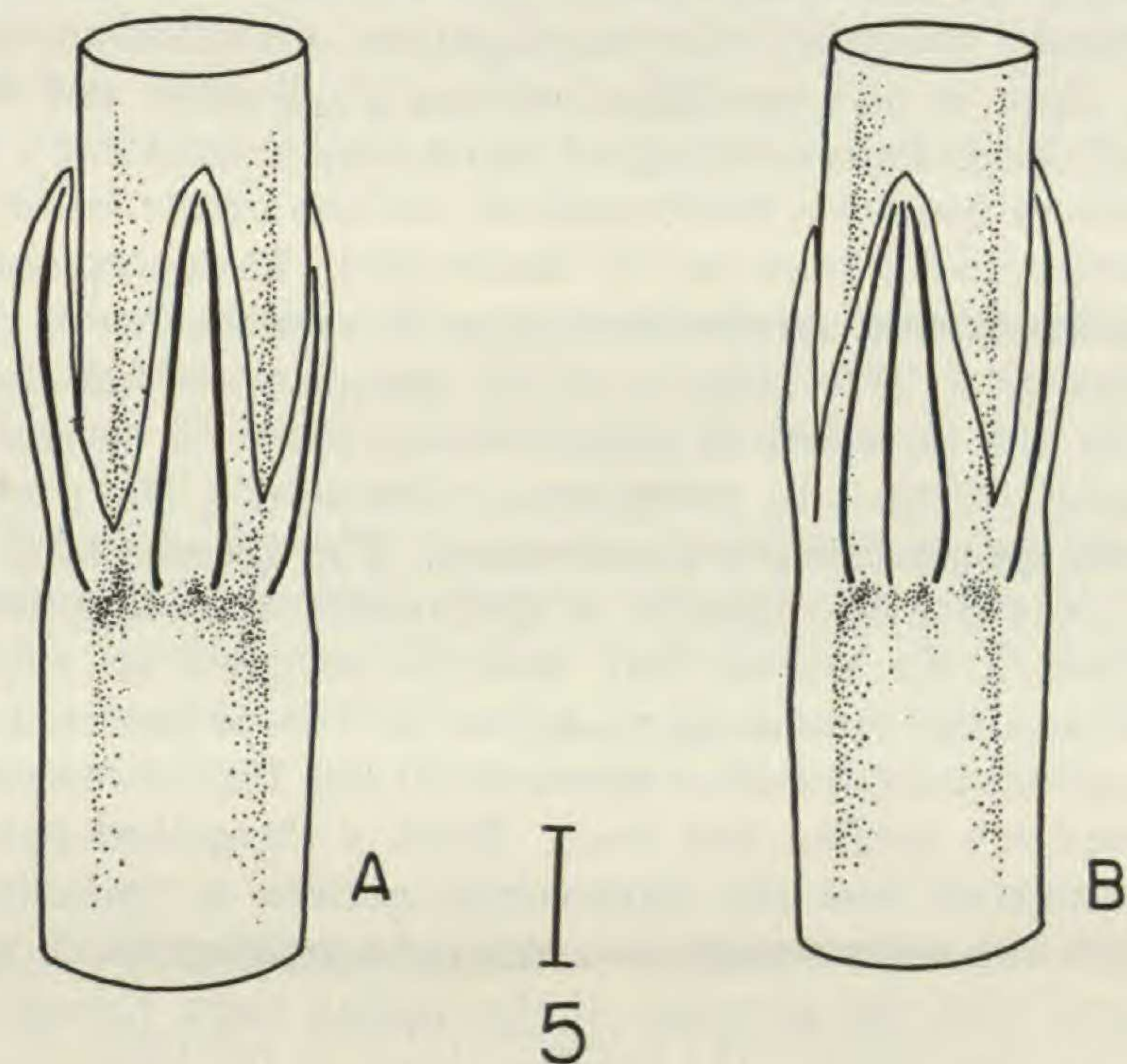

FIGURE 5, A, B. *Ephedra chilensis*. Variation in venation pattern among leaves of the same whorl. One leaf (B) is three-veined while each of the other leaves is two-veined (A). The scale between the drawings equals 1 mm.

In the three species which I have studied, "open venation" i.e. the free termination of the vein-tips, may occur in "rudimentary" as well as well-developed laminae, and probably represents the basic condition in the genus as a whole (TEXT-FIG. 1–5; PLATE I: 1, PLATE II: 5, 6). On the other hand, when transfusion tracheids, which are restricted to the borders of the xylem strands in open venation, subsequently develop *between* the veins, anastomoses are formed. As is shown in PLATE II, the degree of development of transfusion tracheids varies considerably and determines the fluctuation in the levels at which confluence of the veins takes place. In preparations of *Ephedra chilensis*, photographed by combining dark field illumination and transmitted light, the slender xylem-strands of each vein, in the lower part of the leaf, appear as dark lines

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weakly-connate sheaths; note open venation of leaf at right. *axb*, axillary bud, *br*, lateral branch. FIGURE 4, whorl of scale-leaves, detached from shoot and drawn from lower (abaxial) surface. Each leaf is vascularized by a pair of veins and is basally connected, by a prominent commissure, with adjacent leaves of the whorl. The scale at the side of each drawing equals 1 mm.

flanked by massive borders of refractive transfusion tracheids. At the points of lateral union between the veins, the interpolated files of transfusion tracheids are often clearly displayed (PLATES IV, V).

Quite apart from the anatomical contrasts between open and anastomosed venation, there remains the fundamental but difficult question of the significance of the three-veined type of leaf vasculature which occurs in *Ephedra chilensis*. My investigations demonstrate, in the first place, that there is no correlation between phyllotaxis and the number of traces and veins. Pairs or whorls of leaves may be uniformly two-veined, the predominant condition in *E. chilensis*, or one of the leaves at a node may be three-veined (TEXT-FIG. 5; PLATE IV). In my opinion, the reason for this apparently erratic fluctuation in vein-number is obscure, although Monoyer (1937, 1938, a, b, c) has proposed an ingenious explanation for the three-veined pattern in his study of several species of *Ephedra*. In *E. fragilis* var. *campylopoda*, Monoyer (1937) reported that *all* the leaves are consistently three-veined. The absence of a midvein in the leaves of the other species is the result, according to his view, of the failure of the median leaf trace to complete its extension into the leaf. Using the terminology adopted in the present paper, the so-called "complementary bundle," shown in PLATE III, corresponds in position to Monoyer's median leaf trace. From a theoretical point of view, Monoyer concluded that the three-veined pattern is "primitive" whereas a leaf with two veins represents a derived condition which results from the "acrolysis" (i.e. the atrophy) of the median trace (Monoyer 1938 b, p. 60). In his own words, "the bundles absent in the leaves are recovered in the stem in the form of acrolysed strands." (Monoyer 1938 c, p. 64).

Although Monoyer's theory is appealing because of its simplicity, I have found no evidence to support it. If the complementary bundle in the internode represents an incompletely developed median leaf trace, one might expect the occurrence of a "transitional" condition in which the median trace extends *for a short distance* into the leaf sheath. But I have never observed a venation pattern of this sort. On the contrary, the presumptive "arrest" in the development of the midvein occurs in the leaf itself rather than at the node, and is illustrated by appendages in which a median vascular strand terminates blindly at some level in the lamina or sheath (PLATE V: 12; PLATE VI). The venation pattern depicted in PLATE V: 12, suggests that the formation of tracheary elements in the midvein may occur *basipetally* and that the patterns shown in PLATE VI simply represent various degrees in the extent of such basipetal differentiations. This idea, however, because of the absence of ontogenetic data must be considered for the present as entirely speculative.

In angiosperms with unilacunar two-trace nodes the midvein of a foliar appendage may be formed by the union of a pair of central strands which arise as branches of the leaf traces (Bailey 1956). This type of transition from an even to an odd number of major foliar strands was not observed in *Ephedra chilensis*. In the three-veined leaves of this species, the midvein is an independently attached strand, interpolated between the lateral

traces and veins of the leaf (PLATE IV: A). Although the phylogenetic significance of this condition in such a gymnosperm as *Ephedra* is at present an enigma, it is interesting that in *Gnetum Ula*, both the scale-leaves and foliage leaves are vascularized by an odd number (5–7) of discrete leaf traces (Rodin & Paliwal 1970). Direct comparisons between the nodal anatomy of *Gnetum* and *Ephedra*, however, are of questionable value because of the obscure phylogenetic relationship between the two genera (Pearson 1929, p. 143; Eames 1952, p. 97).

There is a great need for a more comprehensive study of leaf venation in *Ephedra* than was possible in the present exploratory survey. The only known examples of three-veined leaves occur in *E. chilensis* and *E. fragilis* var. *campylopoda* which are assigned by Stapf (1889, p. 35) to "Tribus *Antisyphiliticae*" and "Tribus *Scandentes*," under the Section PSEUDOBACCATAE. If Stapf's classification is followed, it is evident that the taxonomic and phylogenetic significance of a trifasciculate type of foliar vasculature in *Ephedra* is an open question pending the results of further comparative studies. Stapf's scholarly monograph, frequently overlooked by modern investigators, describes in detail the leaf morphology and geographical distribution of 31 species of *Ephedra* and provides the essential basis for future surveys of nodal anatomy and venation in this genus.

[POSTSCRIPT TO ORIGINAL MANUSCRIPT]

Professor P. Marten's (1971) treatise, "Les Gnétophytes," came to my attention after the present paper had been completed. He takes the position that the morphological reduction of the leaf in *Ephedra* also involves its vascular system. This, he states, consists of two parallel collateral endarch veins which neither branch nor reunite in their course through the leaf. Although he notes (p. 21) that Monoyer (1937) had reported the occurrence of three-veined leaves in *E. fragilis*, he refrains from making any comment on the possible morphological or phylogenetic significance of this "divergent" pattern of venation.

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EXPLANATION OF PLATES

PLATE I

FIGURES 1–4. Variations in venation patterns of two-veined leaves of *Ephedra*. FIGURE 1. Free termination of veins near apex of leaf of *E. foliata* (*Barkley 32 Ir 2299*, UC). FIGURE 2. Leaf from same herbarium specimen as FIGURE 1, showing apical union between the two veins. FIGURE 3. *E. foliata* (cult. UC Bot. Garden) showing union, some distance below leaf-apex, of the two closely approximated veins. FIGURE 4. *E. altissima* (cult. USDA Plant Intro. Station, Chico, Calif.) showing confluence of the two veins distal to leaf-apex. All figures, × 11.8.

PLATE II

FIGURES 5–8. Details of vein structure in leaf-apices of *Ephedra foliata*. FIGURE 5. Apex of one member of leaf-whorl shown in TEXT-FIG. 4. Note conspicuous transfusion tracheids. FIGURE 6. Apex of leaf shown in PLATE I: 1. Each vein is bordered by abundant transfusion tracheids. FIGURE 7. Apex of leaf shown in PLATE I: 2. The vein-tips are united by a central mass of transfusion tracheids. FIGURE 8. Apex of leaf shown in PLATE I: 3. The two vein-tips are laterally merged, forming a single massive xylem-strand. Note cluster of prominent hairs developed at apex of lamina. All figures, × 62.

PLATE III

FIGURE 9. *Ephedra chilensis*. Cleared and stained longitudinal half of a nodal sector showing the independent attachment of the two leaf traces (*lt*), the nodal girdle composed of transfusion tracheids (*tr*) and the mode of termination at the node of the complementary bundle (*cb*). Note strands of fibers between the two veins of the leaf. × 92.

PLATE IV

FIGURE 10, A, B. *Ephedra chilensis*. A pair of cleared, stained leaves, separated by means of a longitudinal cut through the node and photographed by using a combination of dark field illumination and transmitted light. One leaf (A) is three-veined, with the median vein basally attached to the complementary bundle whereas the other member of the pair (leaf B) is two-veined. Note massive development of transfusion tracheids near the apices of both leaves. × 21.5.

PLATE V

FIGURES 11, 12. Three-veined leaves of *Ephedra chilensis*, photographed with a combination of dark field and transmitted light. FIGURE 11. Leaf showing a very attenuated connection between the median leaf vein and the complementary bundle. The three vein-tips merge with the transfusion tracheids near the leaf apex. FIGURE 12. Leaf illustrating the *blind termination* of the midvein between the bases of the two lateral traces. Note massive development of transfusion tracheids in upper part of lamina. × 26.

PLATE VI

FIGURES 13, 14. Leaves of *Ephedra chilensis* with blindly-terminating midveins, photographed by the combined use of dark field and transmitted light.

FIGURE 13. A detached leaf, showing the termination of the well-developed median vein in the lower part of the leaf sheath. Note transfusion tracheids between midvein and each lateral vein in upper part of lamina. FIGURE 14. Half of a longitudinally divided nodal sector, showing a discrete midvein ending blindly in base of lamina, and the connection of the lateral traces with the stele. Note the refractive appearance of the stomata in the lower portions of both photomicrographs. × 26.

PLATE VII

FIGURES 15, 16. Detailed structure of leaf veins of *Ephedra chilensis*. FIGURE 15. Small sector of lamina of leaf depicted in PLATE IV, A, showing large transfusion tracheids associated with each of the three veins. FIGURE 16. Structure of the blind termination of a suspended midvein. Note the slender tracheary elements of the blind ending and the abundant transfusion tracheids flanking the lateral veins. × 92.
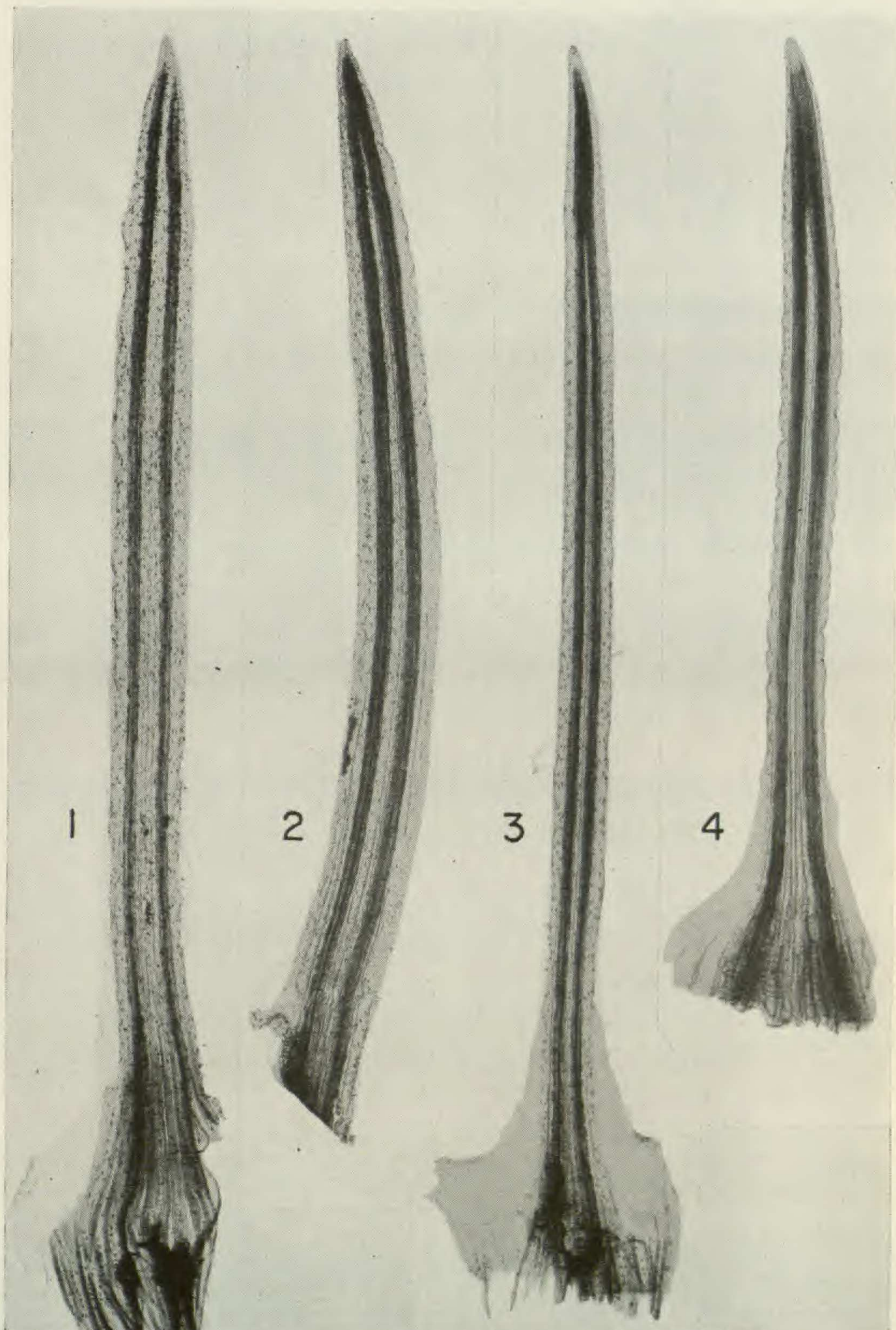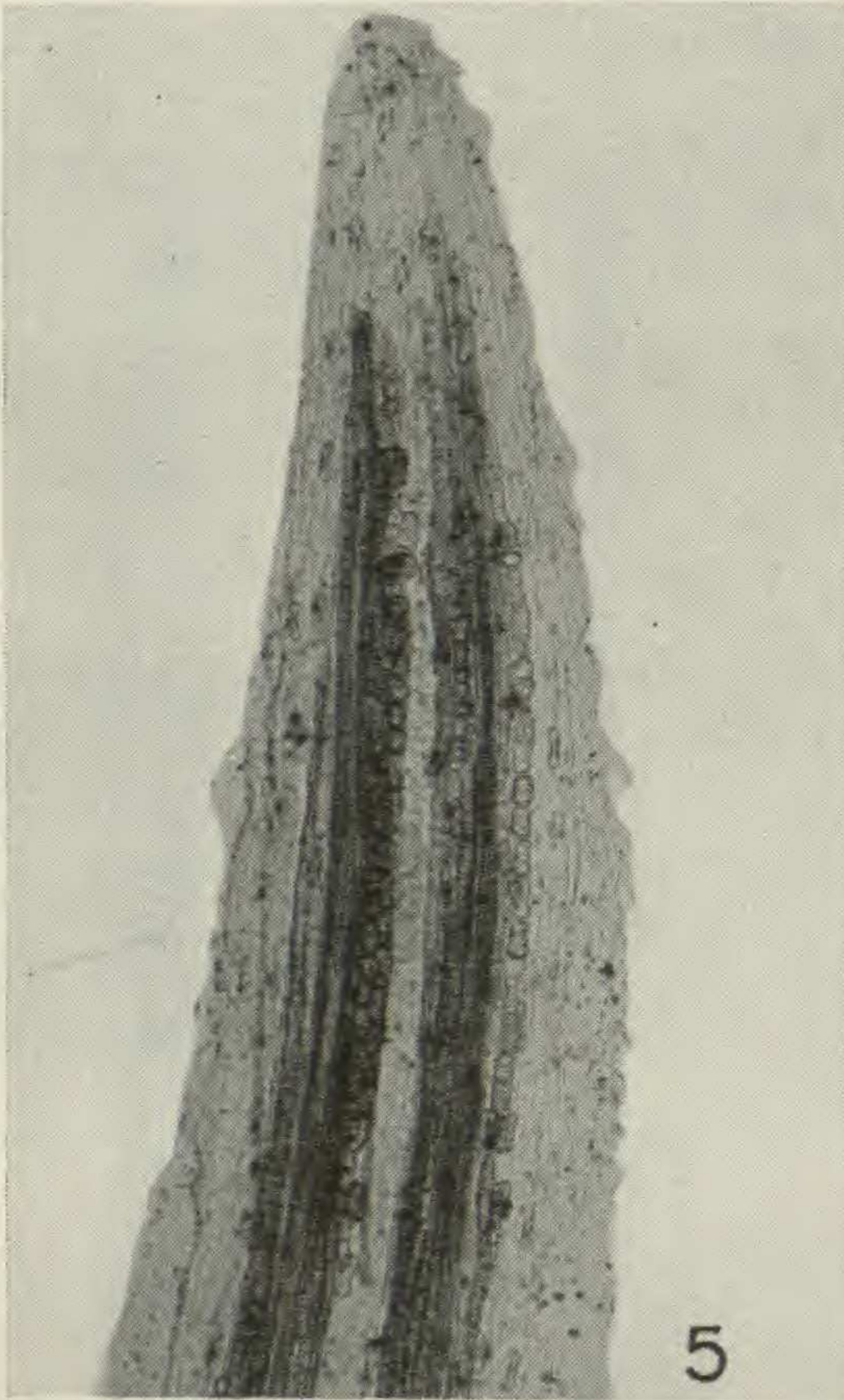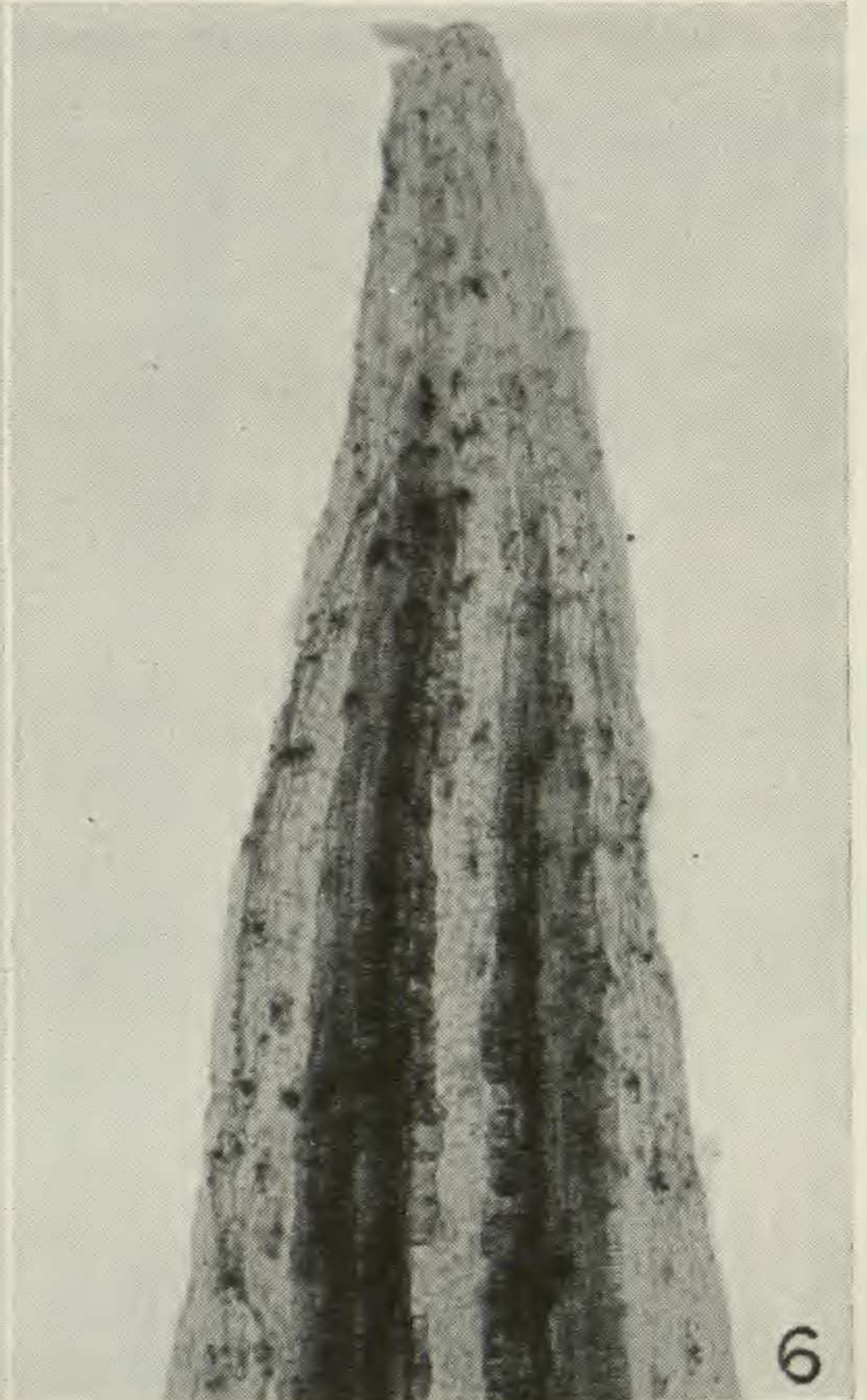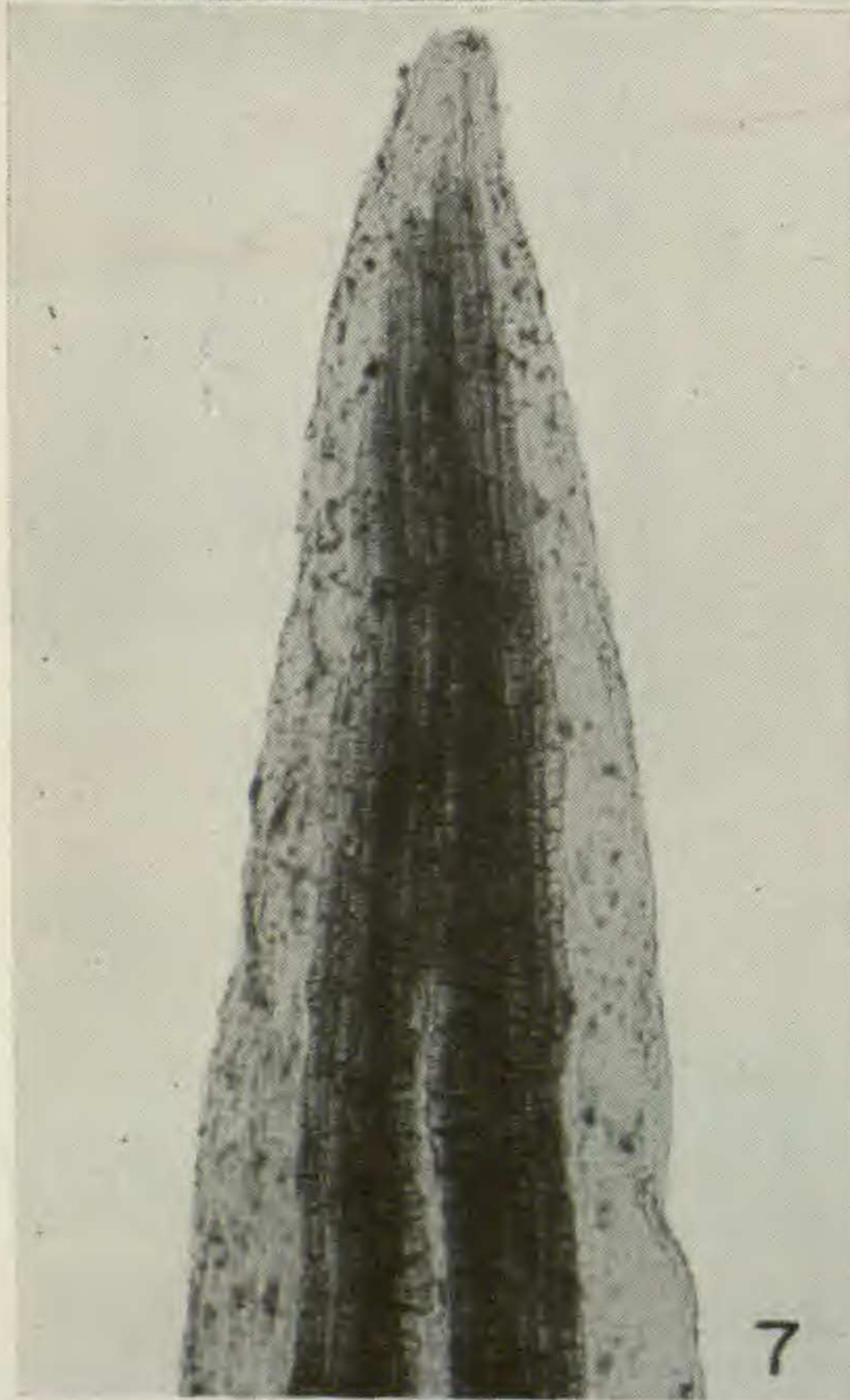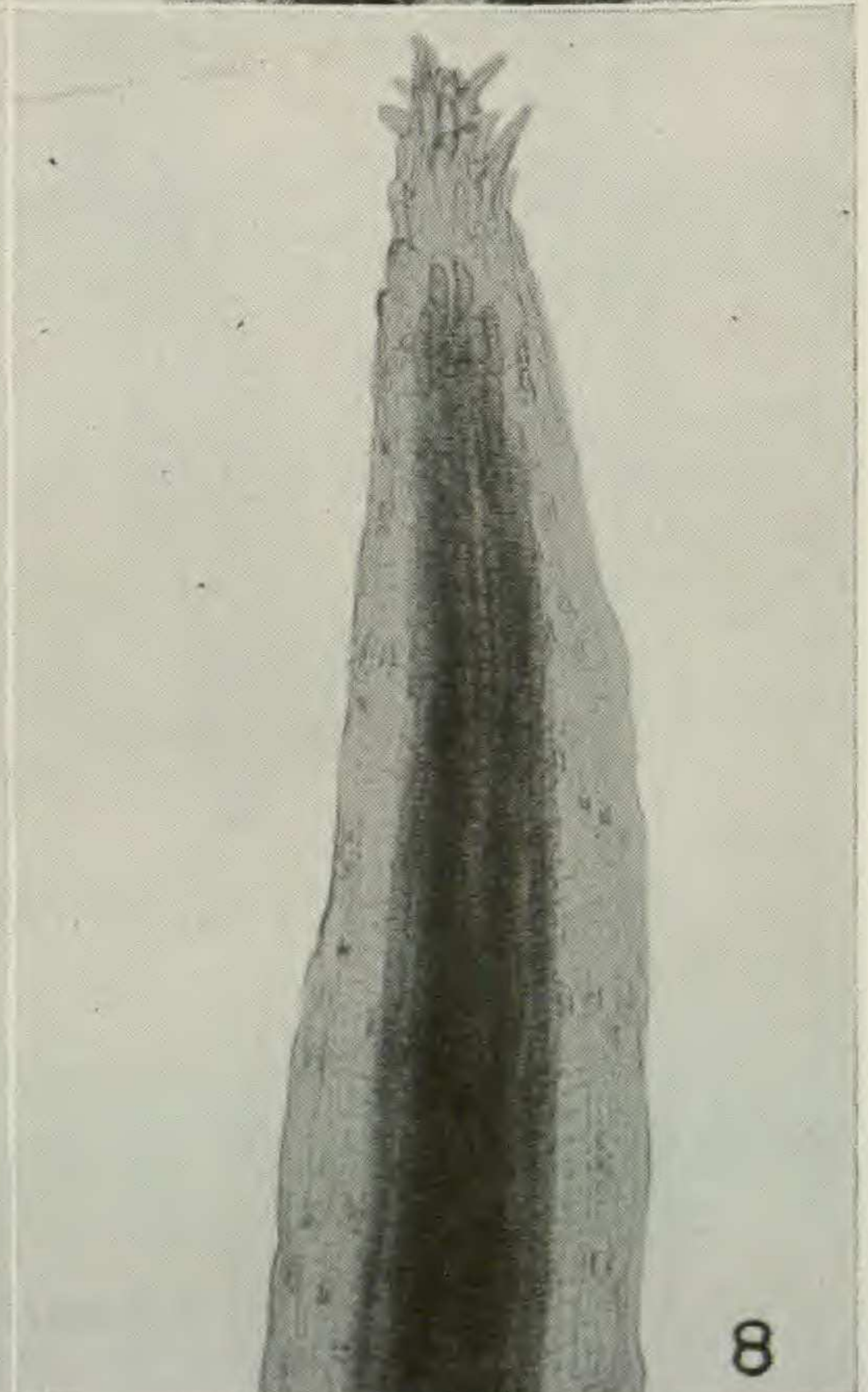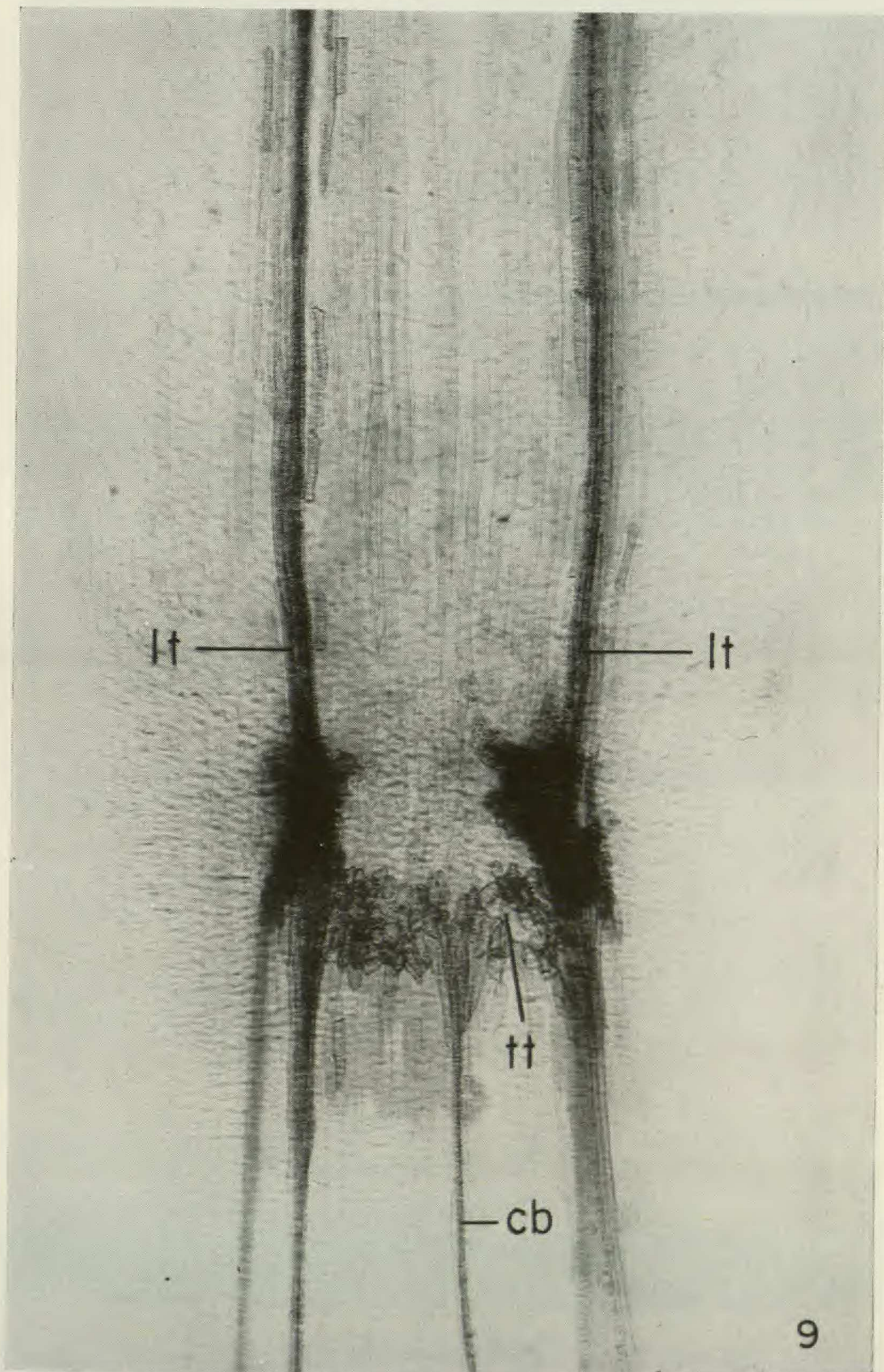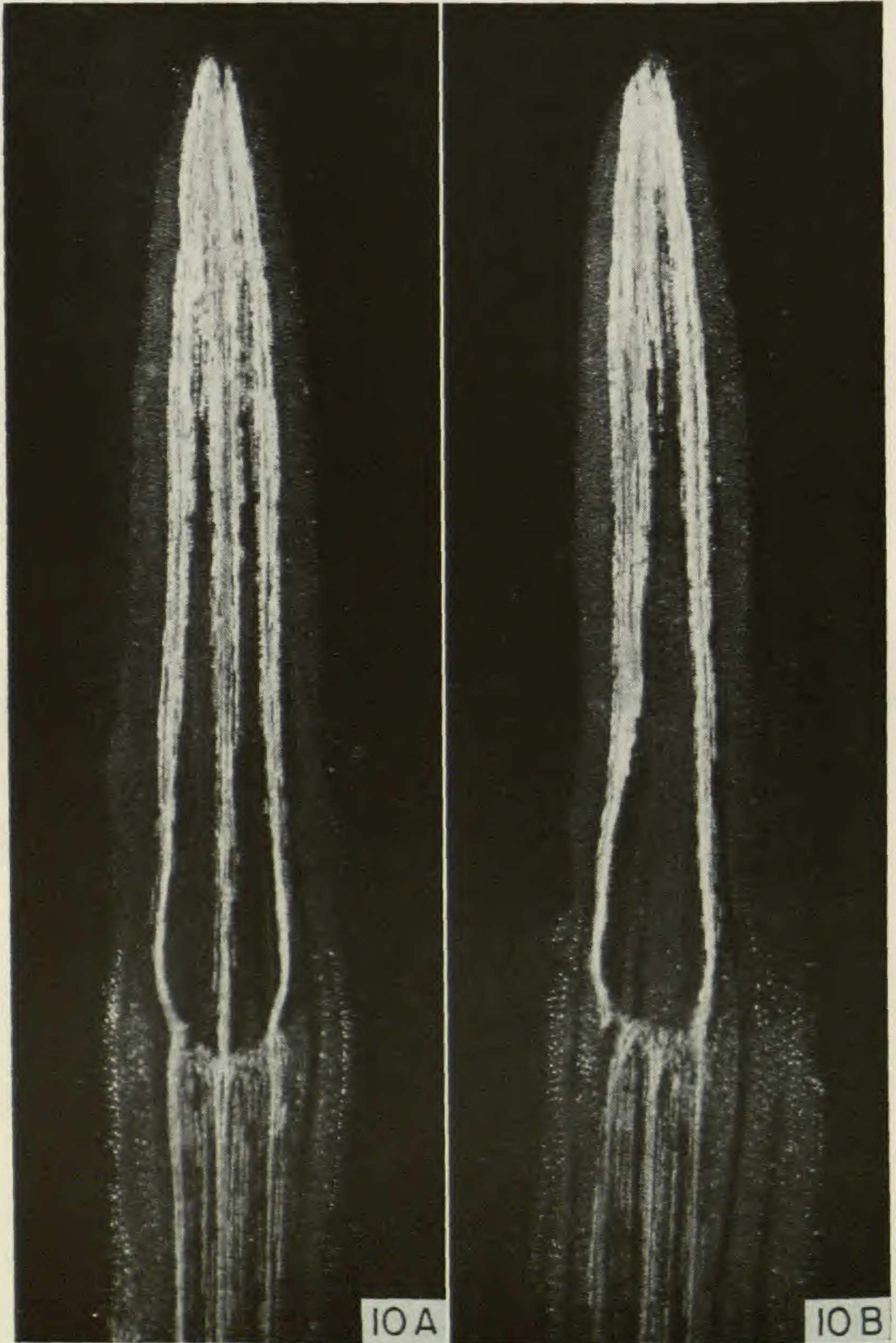
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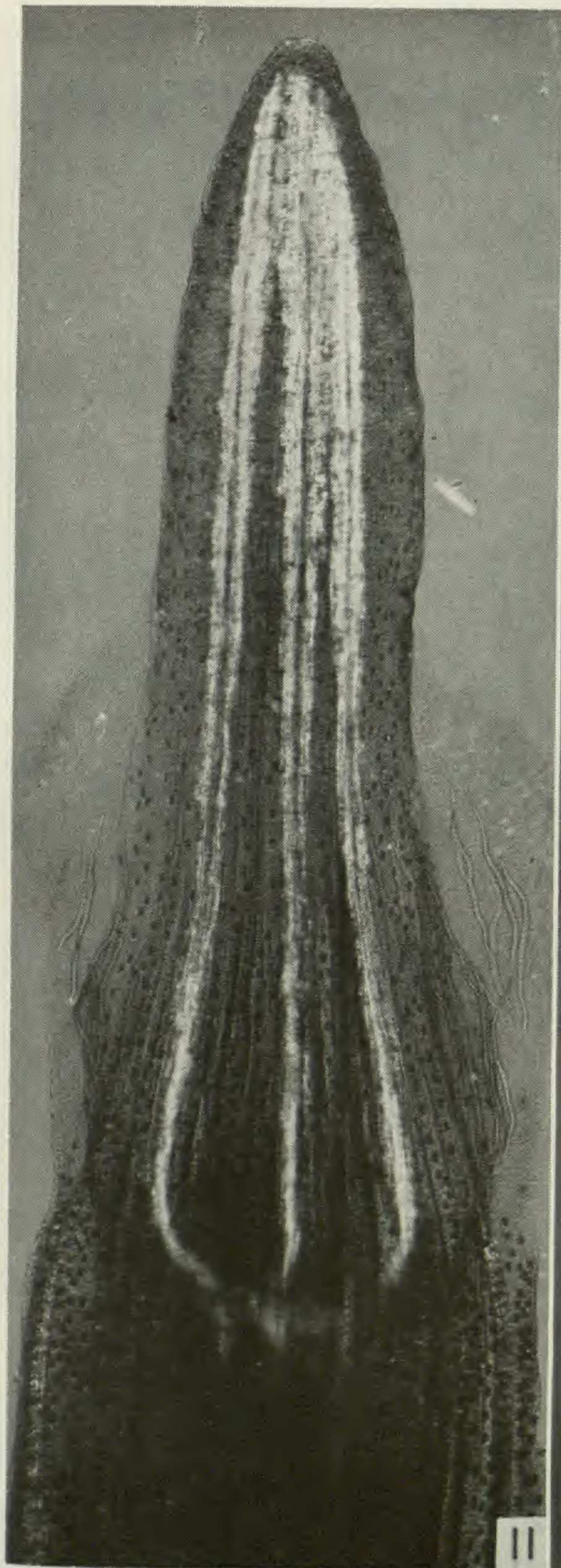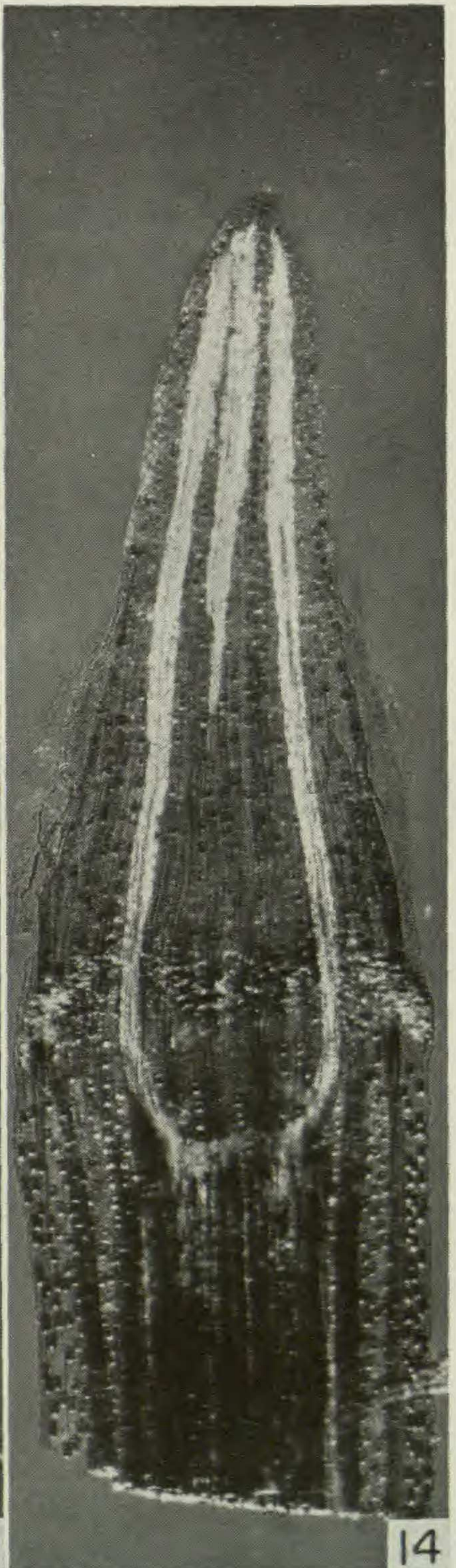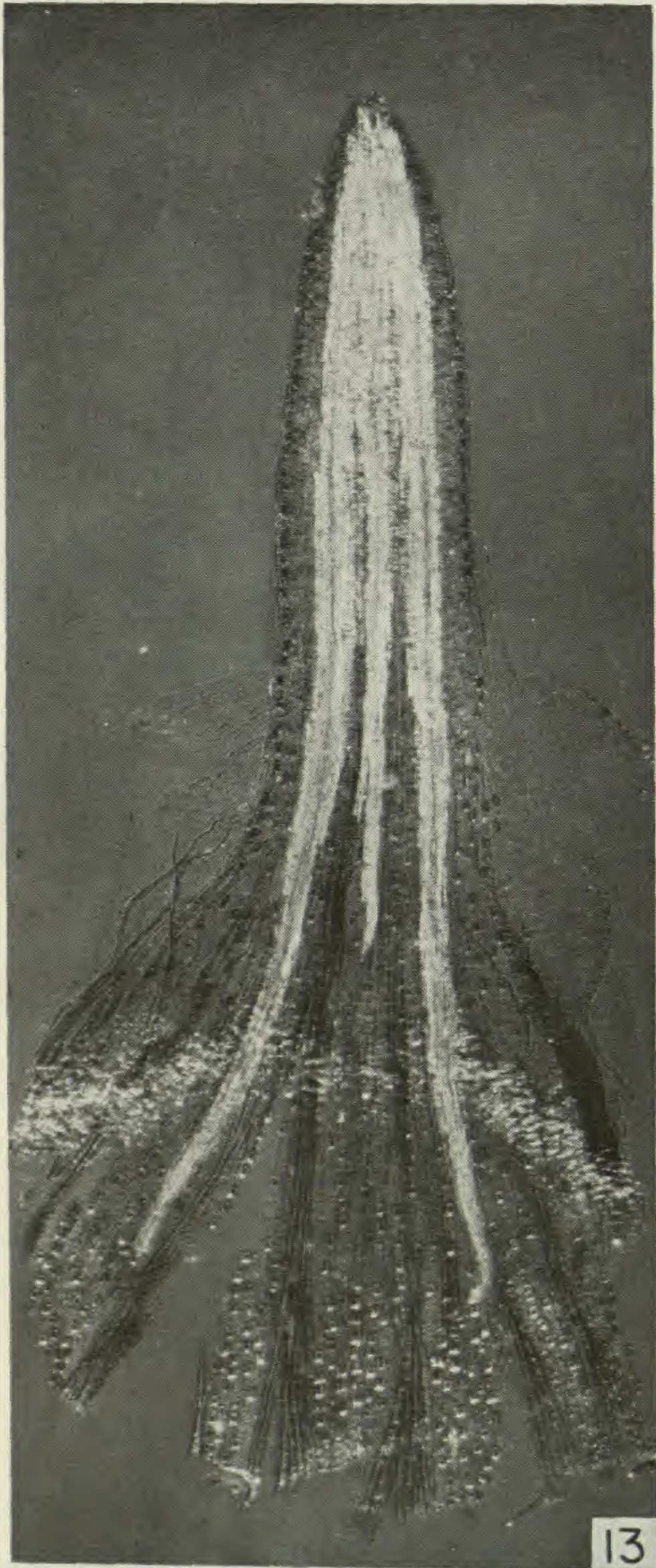
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PLATE VI

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